BIOLOGICAL BULLETIN

THE YPSILOID APPARATUS OF URODELES.

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INTRODUCTION.

Articulated to the anterior margin of the pubis of many sala-manders, there is a cartilage which, from its peculiar Y shape, is known as the *Cartilago ypsiloides.* This cartilage has in general been assumed, by those who have described and figured it, to be identical with the anterior paired or unpaired cartilaginous proc-ess, the *Processus epipubicus* of the *Proteidæ* and *Derotremata.* Thus Wiedersheim in his *Grundriss* (1893, p. 165), says, after speaking of the paired nature of the anlage of the pelvic girdle, " Dies hervorzuheben ist namentlich auch wichtig im Hinblick auf die Morphologische Bedeutung jenes Abschnittes, den ich als *Processus epipubicus* bezeichnet habe. Die ursprünglich paarige Natur desselben tritt bei dem Becken von *Proteus* und *Am-phiuma* zeitlebens deutlich hervor.

" Auch bei den *Derotremen* und *Salamandrinen* findet sich am vorderen Beckenrand in der Medianlinie ein Knorpelfortsatz, der als *Epipubis* zu betrachten ist, und in manchen Fällen lässt sich dessen directer Zusammenhang mit der eigentlichen Beckenplatte noch deutlich nachweisen. Insofern aber liegt bereits ein Fall von sogenannter abgekurzter Entwicklung vor, als der *Processus epipubicus* hier nicht mehr paarig, sondern als ein unpaarer Aus-wuchs sich an seinem Vorderende erst secundär gabelig theilt."

Gegenbaur, also, in his " Vergleichende Anatomie " (1898, Vol. I., p. 550), after describing the pelvic girdle of *Necturus* with its long anterier process says that " Derselbe Teil bei Salamandrinen als medianer terminal gegabelter Fortsatz erscheint, das soga-nannte *Epipubis.* Aus der Vergleichung dieser beiden Zustände geht hervor, dass das *Epipubis* bereits in der Platte des Pubis

besteht und nicht als besonderer Fortsatz auftritt. Seine Ent-
stehung geht sonach aus einer bilateralen Reduction eines Teiles
der ventral Beckenplatte hervor."

Hoffmann (Bronn's "Their-reich," Bd. 6, II., Amphibien,
1873–8, p. 77), says in his description of the pelvic girdle of
Urodeles, " Der vordere Rand des Schamsitzbeins verlängert sich
nach vorn in eine mediane Spitze. Bei *Proteus* und *Meno-
branchus* ist diese Spitze mit der ventralen Platte continuirlich ver-
bunden, wahrend sie bei den anderen Urodelen durch Syndesmose
damit innig zusammenhängt. Dieser ventrale Fortsatz, welcher
bei *Proteus, Menobranchus,* und *Amphiuma* nur sehr kurz ist,
verlängert sich bei den anderen Urodelen in die ventrale Muskel-
masse und spaltet sich vorn gabelförmig in zwei divergirende
Schenkel (*Cartilago ypsiloides*). Bei *Cryptobranchus japonicus,*
wo dieser ventrale Fortsatz der knorpeligen *Epiphyse* der Scham-
beinplatte aufsitzt, ist desser rechter Schenkel in drei Sipfen [*sic*]
gespalten, welche jedoch am linken Schenkel fehlen."

In all of the above quoted authorities it is implied or assumed
that the epipubic cartilage (*Cartilago ypsiloides*) occurs universally
in *Urodeles.* Wiedersheim ('75), however, in his work on
Salamandrina perspicillata and *Geotriton fuscus* (p. 142), under
the heading *Cartilago ypsiloides* expresses himself as greatly sur-
prised at finding no trace of the cartilage in *Geotriton,* adding,
" Wo also die Erklarung zu suchen ist, ist mir dunkel gebleiben,
doch wäre vielleicht von der Untersuchung der Larven, welche
mir im Augenblick nicht bei der Hand waren, noch etwas zu
erwarten " ; and recently Miss Emerson in her work on the anat-
omy of *Typhlomolge rathbuni* (1905) mentions the absence of the
Cartilago ypsiloides in that species.

The following tabulated results of my own dissection of the
pelvic region of salamanders[1] shows, moreover, that the *Car-
tilago ypsiloides* is far from being universal in occurrence :

Cartilago ypsiloides, present.	*Cartilago ypsiloides*, absent.
Triton alpestris,	*Desmognathus fusca,*
Triton helveticus,	*Batracoseps attenuatus,*
Diemyctylus viridescens,	*Spelerpes ruber,*

[1] The term salamander is used here as synomymous with the suborder Salamandrida,
comprising all of the Urodeles except the Derotremata and Perennibranchiata.

Cartilago ypsiloides, present.

Amblystoma opacum,
Amblystoma punctatum,
Amblystoma jeffersonianum,
Amblystoma talpoideum,
Salamandra maculosa,
Salamandrina perspicillata.

Cartilago ypsiloides, absent.

Spelerpes bilineatus,
Spelerpes guttolineatus,
Spelerpes porphyriticus,
Spelerpes longecaudus,
Manculus quadridigitatus,
Plethodon cinereus,
Plethodon erythronotus,
Autodax lugubris.

In those forms in which the cartilage is present it exhibits the typical Y-shaped character, and is movably articulated to the anterior edge of the pubis.   In the species given in the right-hand column there is no trace of the cartilage whatsoever. These results show that the presence of a *Cartilago ypsiloides* is closely correlated with the presence of lungs, although there seem to be two exceptions, viz., *Amblystoma opacum* and *Salamandrina perspicillata*.   The first of these, however, rests upon an error, since the *Amblystoma opacum*, like the others of its genus, possesses large and well developed lungs, although through the authority of Lönnberg ('96) this species has for several years been placed among lungless forms.   It is impossible to say through what appearances Lönnburg was deceived, but the presence of well developed lungs has been repeatedly demonstrated by me through dissection and physiological experiment. The most plausible hypothesis is that he was mistaken in his species, an error extremely likely to occur in the study of this group.

Marked differences in the activities of lungless and lunged salamanders when in the water, a subject which will receive full discussion later, further corroborate the view that the function of the ypsiloid cartilage is correlated with that of the lungs.   In fact, it was this difference in activity which first called my attention to the difference in anatomy and led me to make an extensive study of the ventral pelvic region of *Urodeles*.

PART I. ANATOMY OF THE YPSILOID REGION IN URODELES.

A. *Description of Adult Forms.*

1. *Diemyctylus viridescens.*—In *Diemyctylus*, as in all *Urodeles*, the muscular abdominal walls are differentiated into the four typical layers, viz., *Musculus obliquus externus, M. obliquus internus, M. rectus abdominis* and *M. transversalis.* The external oblique is strongly developed, showing the typical outer and inner laminæ. The outer has lost its metamerism except in its origin ; its fibers, which form a strong, continuous, muscular sheet, are mainly inserted into a wide, ventral aponeurosis, and the posterior bundles into ilium and pubis. The rectus abdominis consists of a narrow band of muscle, lying on either side of and contiguous to the linea alba and covered ventrally by the aponeurosis of the obliquus externus. It is very primitive in character, consisting of a series of myotomes, separated by well formed myocommata. The obliquus internus is almost vestigial and in some individuals I was unable to find it. Its very thin layers of fibers arise mainly by digitations from myocommata beneath the deeper layer of the external oblique, although the more posterior bundles have their origin in the anterior edge of ilium and pubis. The fibers of this muscle extend very obliquely, anteriorly and ventrally and are inserted into myocommata. At the edge of the rectus abdominis muscle the fibers of the internal oblique seem in some cases to become continuous with those of the rectus, in other cases to pass dorsal to the rectus, which, however, they only slighly overlap.

The transversalis, even more than the obliquus externus, consists of a continuous muscular sheet, its metamerism being evident only in its origin. It is inserted ventrally into an aponeurosis which is somewhat narrower than that of the obliquus externus and which lies on the inner (*i. e.*, dorsal) surface of the rectus abdominis. This aponeurosis narrows abruptly in the two metameres anterior to the pubis, and ends at the pubic symphysis in a point.

In the two myotomes immediately anterior to the pelvic girdle there is considerable muscular differentiation, which may be most easily shown by a series of dissections. Fig. 1 shows a ventral

view of the posterior abdominal region, with the skin and external oblique muscle removed from the left side. In the mid line, extending anteriorly from the pubic symphysis through the width of a single myotome is the stem portion of the *Cartilago ypsiloides* (*y*), the two lateral arms of which are hidden by the rectus abdominis. The first myotome of the rectus abdominis, counting anteriorly from the pelvic girdle, is differentiated superficially into two portions, the more ventral and lateral of which (*ra*) extends outward with its fibers converging to their insertion into a process at the outer edge of the pubis, which I shall call the *lateral process* of the pubis. This portion is well differentiated into a distinct muscle, and in its insertion is closely associated with the posterior portion of the external oblique. The second portion (*rb*) is partially covered by the first, and its fibers slant medially to their insertion into the ventral surface of the
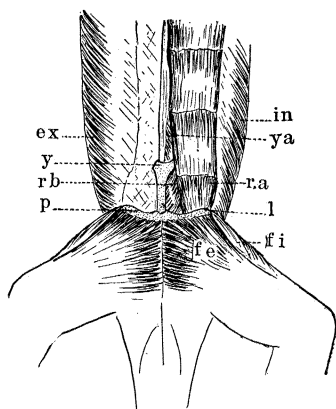

FIG. 1. Ventral view of *Diemyctylus viridescens*, posterior abdominal region, $\times$ 3. The external oblique muscle has been removed from the left side. Abbreviations : *ex*, M. obliquus externus ; *fe*, M. pubo-ischio-femoralis externus ; *fi*, M. pubo-ischio-femoralis internus ; *in*, M. obliquus internus ; *l*, lateral process of pubis ; *p*, pubis ; *ra*, and *rb*, differentiations of the first myotome of the rectus abdominis ; *y*, ypsiloid cartilage ; *ya*, M. ypsiloideus anterior.

stem of the ypsiloid cartilage and the anterior margin of the pubis. When the more ventral of these two muscles is removed, it is found that the medial portion of the deeper muscle takes its origin from the lateral arm of the ypsiloid cartilage, which extends obliquely nearly across the second myotome. In Fig. 2 both of these muscles have been removed, as well as that portion of the second myotome which lies over but unattached to the *Cartilago ypsiloides*. On the right side in the figure may be seen two muscles connected with the cartilage. One of these, which may be designated the *M. ypsiloideus posterior* (*yp*), is a strongly developed muscle which arises from the anterior margin

of the pubis, its thickest portion having its origin in the lateral process. The fibers of this muscle diverge slightly, and are inserted into the edge of the lateral arm, and the inner (*i. e.*, dorsal) surface of the stem of the *Cartilago ypsiloides*. Lying, as it does, dorsal to the main mass of the rectus abdominis, this muscle is almost conti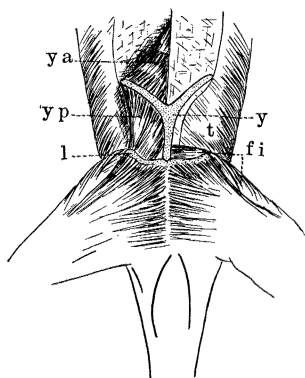nuous at its lateral boundary with the obliquus internus. It is the muscle which has been often called the pyramidalis. Thus Hoffmann described it as a part of the general urodele musculature and homologized it with the pyramidalis of human anatomy.

FIG. 2. Ventral view of *Diemyctylus viridescens*, posterior abdominal region, × 3. All of the abdominal muscles have been removed except the tranversalis muscles and the ypsiloid muscles of the right side. Abbreviations not previously explained : *t*, M. transversalis abdominis ; *yp*, M. ypsiloideus posterior.

The other ypsiloid muscle, *M. ypsiloideus anterior* (*ya*), arises from the medial portion of the second myocomma, and from the linea alba of the first metamere, and its fibers extend obliquely outward and posteriorly to their insertion into the anterior edge of the lateral arm of the cartilage.

The transversalis muscle shows a wide range of individual variation in its relation to the ypsiloid cartilage. In some of the specimens dissected none of its fibers were inserted into the cartilage. The posterior narrowing of the aponeurosis of the transversalis in this region, however, causes the edges of the aponeurosis to lie closely parallel with the outer edges of the ypsiloid cartilage, and in the majority of the specimens dissected some of the fibers of this muscle had become inserted into the cartilage, the ends of the lateral arms being the region where this insertion most frequently occurs. The extent of the insertion of this ypsiloid portion of the transversalis varies, however, from one which involves the outer portion of the arm only, to one which extends along nearly the entire length of the cartilage, both arm and stem (Fig. 3, *tb*). Almost invariably a few fibers of the

muscle immediately anterior to the cartilage extend farther medially than those of the rest of the muscle and may even be inserted into the second myocomma in association with those of the *M. ypsiloideus anterior* (Fig. 3, *ta*).

It should perhaps be emphasized that the entire musculature of the ypsiloid cartilage, while in all cases strongly developed, shows a considerable amount of individual variation, as if the apparatus were one of relatively recent origin and still in the experimental stage of physiological adaptation. The most definite of the muscles involved is the *M. ypsiloideus posterior*.

In addition to the above described musculature of the *Cartilago ypsiloides*, the posterior portion of the stem of the cartilage forms the origin of the anterior portion of the *M. pubo-ischio-femoralis internus*. This muscle takes its origin mainly from the mid ventral line of the pubo-ischium, and that portion which arises from the ypsiloid cartilage extends between the posterior ypsiloid muscle and the transversalis (Figs. 1, 2, and 3, *fi*).

FIG. 3. Dorsal view (*i. e.* from within body cavity showing the muscles attached to the ypsiloid cartilage of *Diemyctylus viridescens*, ×5. On the right side the anterior part of the M. pubo-ischio-femoralis internus has been cut away. Abbreviations not previously explained: *ta*, the portion of the transversalis inserted into the second myocomma; *tb*, the portion of the transversalis which is inserted into the ypsiloid cartilage.

2. *Triton helveticus, T. alpestris, Salamandra maculosa, Amblystoma opacum, A. punctatum.*—Although representing different subfamilies, these forms so closely resemble *Diemyctylus* in the anatomy of the ypsiloid region that they may be grouped together in this comparison. The *Tritons* most closely resemble *Diemyctylus*, the correspondence part for part being almost exact. *Salamandra* and the *Amblystomas* have a relatively less strongly developed external oblique, while the rectus abdominis is broader and more powerful and the internal oblique more strongly developed. The differentiations in connection with the ypsiloid cartilage (Fig. 4), are, however, practically the same as in *Diemyctylus*. The *M. ypsiloideus anterior* presents less deviation from the longitudinal course of the rectus abdominis, almost all
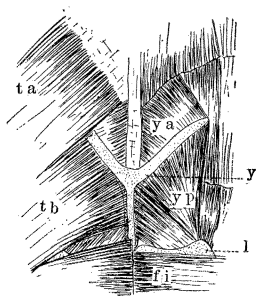
of its fibers proceeding from the myocomma instead of the linea alba. The transversalis shows about the same range of variation that was described in *Diemyctylus ;* the edges of its aponeurosis coincide more exactly with those of the cartilage and in one very muscular specimen of *Amblyst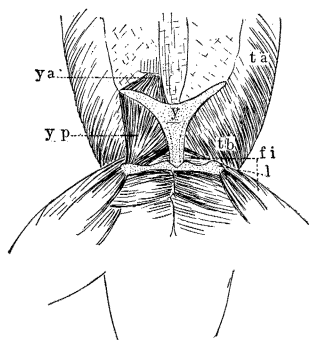oma punctatum*, this muscle was strongly inserted into the cartilage along the whole length of its arm. In the same individual the cartilage was very large, as its arm crossed the second myotome, and the lateral portion of the *M. ypsiloideus anterior* rose from the third myocomma thus giving this muscle an origin from two myocommata.

In all of these genera as in *Diemyctylus* the *M. pubo-ischio-femoralis internus* takes its origin partly from the posterior end of the ypsiloid cartilage.

FIG. 4. Ventral view showing the ypsiloid apparatus of *Amblystoma punctatum*, $\times$ 2. Dissection and abbreviations as in Fig. 2.

3. *Salamandrina perspicillata.* — This species, which, so far as is known, is the only lungless member of the subfamily *Mecodonta*, is sufficiently different in its abdominal musculature from the lunged forms already described, to require a separate discussion. The outer, deeper portion of the rectus abdominis (the rectus profundis of Maurer's nomenclature), is highly specialized into a retractor of the tongue (*M. pubo-hyoideus*). It lies in a sheath, in which it moves freely, since although it possesses myocommata corresponding to those of the remaining portion of the rectus abdominis, these are wholly disconnected from those of the main mass of somatic muscles and thus do not correspond with the latter during all phases of muscular contraction. Aside from this highly specialized region, the abdominal muscles of *Salamandrina* are poorly developed. The external oblique muscle seems reduced almost to a mere sheet of connective tissue, and is evidently functional more as a support for the abdominal wall than for any muscular activity. The internal oblique I have been unable to demonstrate. The rectus abdominis is thin and its two halves are separated by a very wide line

alba. It does not show in the myotome anterior to the pubis the superficial differentiation noted in the forms already described. Neither is any of this superficial portion attached to the ypsiloid cartilage.

The musculature of the *Cartilago ypsiloides* is otherwise quite similar to that of *Diemyctylus*. The anterior ypsiloid muscle, is, owing to the great width of the linea alba, inserted into the distal portion only of the arms. The relation of the *M. pubo-ischio-femoralis internus* to the ypsiloid cartilage is the same as that already described in the preceding cases.

4. *Desmognathus brimleyorum, D. fusca, Spelerpes ruber, S. bilineatus, Plethodon erythronotus, P. cinereus.*— In none of these forms is there a *Cartilago ypsiloides*. The musculature of the posterior abdominal region gives, however, decided evidence of the former existence of an ypsiloid apparatus.

FIG. 5. Ventral view of the posterior abdominal region of *Desmognathus brimleyorum*, × 2. The M. obliquus externus has been removed from both sides and the M. pubo-ischio-femoralis externus from the right side.

The abdominal wall shows a more primitive musculature than *Diemyctylus*, the metamerism being much more strongly marked. The rectus abdominis is broad and powerful. In the myotome (Fig. 5, *r*) immediately anterior to the pubis there is the same superficial differentiation that *Diemyctylus* and other lunged forms exhibit. There is one difference, however, which is due to the fact that the anterior border of the pelvic girdle is deeply incurved on either side of the ventral midline so that the border presents a conspicuous median and two lateral processes (Fig. 6, *l* and *m*). As a result of this the medial portion of the rectus abdominis extends much farther posteriorly than the lateral portion, since it is inserted into the ventral surface of the girdle somewhat posterior to this incurved edge.

In all of the lungless forms dissected the deeper portion of the first myotome of the rectus abdominis shows a well defined though not at all strongly developed portion (Fig. 6, *ypv*) which
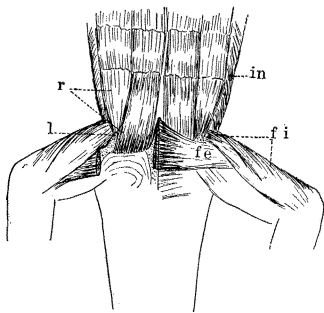
arises from the lateral process of the pubis. From this origin the fibers diverge to their insertion mainly into the linea alba, although in most cases a few are inserted into the first myocomma. When we consider the *Cartilago ypsiloides* of the lunged forms, with its stem in the linea alba and its arms diverging at the first myocomma, it seems very probable that this muscle in the lungless forms is a vest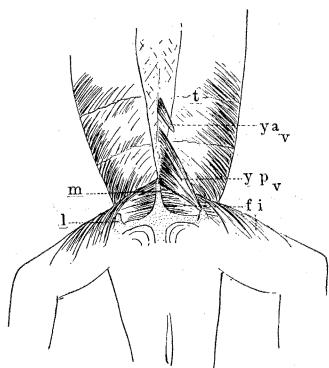igial *M. ypsiloideus posterior* which persists even after the disappearance of the cartilage to which it was originally attached. In some specimens a few fibers of this muscle were found to extend to the second myocomma and in one specimen of *Desmognathus brimleyorum* a separate little muscle (Fig. 6, *yav*) consisting of a few fibers only was found in the region of the second myotome arising in the linea alba and converging obliquely outward and posteriorly. These variable evidences of differentiation from the second myotome suggest, of course, the probable vestiges of the *M. ypsiloideus anterior*.

FIG. 6. Ventral view of the posterior abdominal region of *Desmognathus brimleyorum*, × 2. All of the abdominal muscles have been removed except the transversalis muscles and the vestigial ypsiloid muscles of the left side. Abbreviations not previously explained : *m*, median process of pubis ; *ya_v*, vestige of anterior ypsiloid muscle ; *yp_v*, vestige of posterior ypsiloid muscle.

Still further evidence of the former existence of an ypsiloid cartilage in lungless forms is furnished by the fact that in its absence the anterior portion of the *M. pubo-ischio-femoralis internus* originates from the linea alba in the exact region corresponding to the origin from the posterior part of the stem of the ypsiloid cartilage in lunged forms.

5. *Cryptobranchus allegheniensis.* — In *Cryptobranchus* the ypsiloid cartilage is very well developed and its articulation with the pubis displays marked mobility. It differs somewhat in form from that of the salamanders, in that its lateral arms are very much longer and rapidly broaden toward the outer ends so that they are spatulate in shape (Fig. 7). The cartilage begins to

fork slightly anterior to the first myocomma and the lateral arms extend obliquely across the third myotome.

The musculature of the cartilage is interesting. Superficially, the first myotome of the rectus abdominis is imperfectly differentiated into two portions, and the medial fibers not only of the
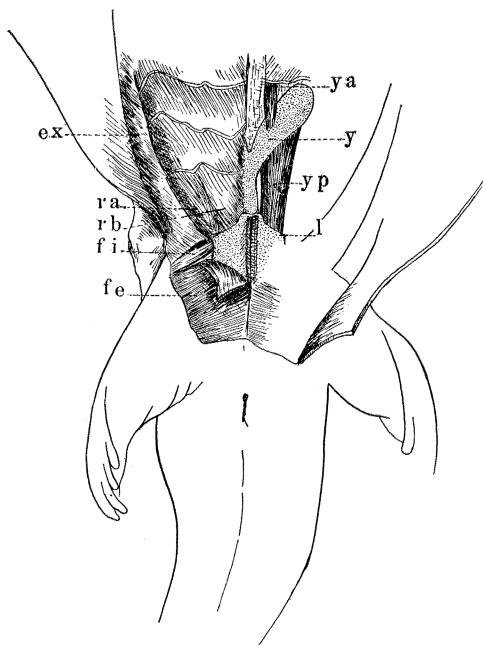
FIG. 7. Dissection of *Cryptobranchus allegheniensis* showing the ypsiloid cartilage and the muscles associated with it, $\times$ 2½. The external oblique and rectus abdominis muscles have been removed from the left side. Abbreviations as in previous figures.

first but of the second myotome are inserted into the stem of the cartilage, the more anterior fibers of the second monotome, however, being inserted into the ventral surface of the cartilage at the very base of the arms.

The deeper layers show a strongly developed *M. ypsiloideus posterior*, differing from that of the forms already described in that its insertion into the *Cartilago ypsiloides* extends only about two thirds the length of the arm, the thin, expanded, outer third of the arm being free from all muscular attachment. The most medial fibers of the third myotome

extend as a small bundle from the third myocomma to an inser-
tion into the middle of the ventral surface of the lateral arm of
the cartilage. This differentiation from the third myotome is the
only representative of a *M. ypsiloides anterior*, and except for its
insertion it is not at all distinct from the adjoining fibers of the
myotome.

None of the fibers of the transversalis are inserted into the
ypsiloid cartilage. The edges of its aponeurosis in this region,
however, are parallel with the cartilage and separated from it by
a space about equal to the
width of the cartilage itself.
Moreover, the stem and proxi-
mal third of the arms of the
cartilage are firmly bound to
the aponeurosis; the portion
of the cartilage involved in
this attachment is much
thicker than the free, distal,
expanded region of the carti-
lage which lies in the third
myotome in a sort of sheath
between the aponeurosis of
the transversalis and the deep-
er layers of the rectus abdo-
minis and has neither muscu-
lar nor aponeurotic attach-
ments.

FIG. 8. Dissection of *Necturus macu-
latus* showing a ventral view of the pelvic
region, with the *M. pubo-ischio-femoralis
externus* of the left side removed, $\times$ 1.
Abbreviations as in previous figures.

[From an unpublished drawing by H.
H. Wilder.]

The origin of the anterior portion of the *M. pubo-ischio-femo-
ralis internus* does not involve the ypsiloid cartilage, although it
extends to the extreme anterior margin of the pubo-ischium.

It should be mentioned in connection with this description of
Cryptobranchus allegheniensis that Hyrtl ('65) has described the
ypsiloid cartilage of *Cryptobranchus japonicus* as lacking bilateral
symmetry in that the right lateral arm is subdivided into three
branches while the left is simple. This description was, I suppose,
based upon a single individual and the condition was quite prob-
ably an abnormal one.

6. *Necturus maculatus.* — In *Necturus* there is no vestige what-ever of a *Cartilago ypsiloides.* The pubo-ischium is produced anteriorly into a long median point (the epipubic process of previous writers), the sides of which slant gradually posterio-laterally to the outer angle of the pelvis where a lateral process is slightly developed (Fig. 8). The first myotome of the rectus abdominis muscle is correspondingly narrow at the ventral mid-line, and much wider toward its lateral boundary. Its fibers are inserted along the entire anterior margin of the pubo-ischium and show a differentiation into a medial (rb) and a lateral portion (ra), the latter inserted into the lateral portion of the pubis. In some specimens this lateral portion is more distinct than in others, and occasionally assumes the character of a semi-independent muscle, as in *Diemyctylus.* There is no indication whatever of a muscle dorsal to the main mass of the rectus abdominis and in-serted into the linea alba, to suggest a vestigial ypsiloid muscu-lature. The *M. pubo-ischio-femoralis internus* moreover, has its origin wholly from the pubo-ischium instead of arising in part from the linea alba as it does in the case of the lungless sala-manders. There is therefore absolutely no indication of the previous existence of a *Cartilago ypsiloides* in this species.

7. *Amphiuma means.* —*Amphiuma means* shows a similar failure of all trace of an ypsiloid apparatus. The pubo-ischium lacks a mid-ventral symphysis in this form and there is only a slight an-terior prolongation of the cartilage on either side of the mid-ventral line where the two halves of the girdle are in contact. The muscular differentiation in this region is, however, practically similar to that already described for *Necturus.*

8. *Siren lacertina.* — This species not only shows no trace of a pelvic girdle and appendages, but, as might be expected, there is also no muscular differentiation to indicate the former presence of an ypsiloid apparatus.

B. *Development of the Ypsiloid Apparatus.*

My material for the study of the development of the ypsiloid apparatus was somewhat limited. It consisted of (1) larvæ of *Amblystoma opacum* — various stages from 37 to 50 mm. in length ; (2) a series of horizontal sections of the larvæ of *Triton*

alpestris, length from tip of snout to cloaca, 13 mm.; (3) small specimens of *Diemyctylus viridescens* in the terrestrial stage, 32–68 mm. in length ; (4) larvæ of *Spelerpes ruber*, and *Spelerpes bilineatus ;* (5) larvæ of *Desmognathus fusca* from 17:5–25 mm. in length.

The methods employed in the study of these larval forms were (1) dissection of the larger ones, prolonged staining in methylene blue being used in some cases to bring out the cartilage ; (2) staining in borax carmine and clearing *in toto* the ventral wall of the posterior part of the body cavity including the pubo-ischium and proximal portion of the femur ; (3) horizontal serial sections of the ventral body wall ; and (4) transverse serial sections of the posterior part of the body. In the case of each of the younger stages all three of the latter methods were used.

In 37 and 42 mm. long *Amblystoma opacum* larvæ there is no trace of the ypsiloid cartilage. The two halves of the pubo-ischium are quite separate. The muscular abdominal walls show the two primitive laminæ (obliquus externus profundus and obliquus internus) with the rectus abdominis as a ventral continuation of both. In the larger specimens the obliquus externus superficialis and the transversalis appear as secondary developments in the form of very thin laminæ. There is a noticeable difference in size of fiber between the medial well differentiated portion of the rectus abdominis and the more lateral region which grades imperceptibly into the deep external oblique on the outside and the internal oblique within. The latter region of the rectus abdominis (*i. e.*, the rectus abdominis profundus), like the two primitive laminæ with which it is continuous, consists of large fibers two or three times the diameter of those constituting the medial portion of the rectus. The latter are thus easily recognized both in sections and in the *in toto* preparations.

All of these early stages show that in the somite immediately anterior to the pubo-ischium, the inner portion of the rectus abdominis is differentiated into a muscle which deviates sharply from the general longitudinal course of the rectus abdominis. Its fibers, which are small like the rest of the medial portion of the rectus abdominis, arise in the lateral processes and along the anterior edge of the pubis and extend obliquely medially to be

inserted partly into the linea alba of the first somite. From the point where the first myocomma joins the linea alba, the insertion of the muscle follows an outwardly curving line which ends about half way across the second myotome, and thus with the insertion of the corresponding muscle of the opposite side maps out the exact location of the future *Cartilago ypsiloides*. This muscle is evidently the *M. ypsiloideus posterior* and is at this stage the only definite indication of an ypsiloid apparatus.

In *Amblystoma opacum* larvæ of 50 mm. I find that the ypsiloid cartilage has appeared. It possesses practically the adult form and relationship, but is very thin, especially toward the ends of the lateral arms. The stem of the cartilage is quite separate from the pubo-ischium which at this stage still consists of two wholly separate lateral halves. I was unable to obtain larvæ of *Amblystoma opacum* between 42 and 50 mm. in length and can therefore make no statement concerning the earliest appearance of the ypsiloid cartilage. Its entire absence in the 42 mm. stage, however, considered in connection with its complete formation in the 50 mm. stage in which the two halves of the girdle are still separate, points conclusively to the origin of the ypsiloid cartilage independently of the pelvic girdle as a chondrification of the linea alba of the first somite and of the deeper portion of the first myocomma. The possibility of such chondrification of regions of muscular attachments upon which a special strain is brought is well established, and the lack of correspondence in this case between the transverse direction of the myocomma and the curved form of the arms of the cartilage may be looked upon as expressing a resultant of forces, since the arms of the cartilage tend somewhat to follow the direction of the edge of the aponeurosis of the transversalis, the posterior portion of which, we have already seen, is usually eventually inserted into it.

The horizontal series of sections of the *Triton alpestris* larva show a well developed ypsiloid cartilage. This is wholly separate from the pubo-ischium though, as in *Amblystoma*, articulated with it. The two halves of the pubo-ischium are at this stage still quite separate.

All of the specimens of terrestrial *Diemyctylus* which I dis-

sected show the ypsiloid cartilage well developed and with prac-
tically the same muscular attachments as in the adult.

From my necessarily limited study of larval forms, it appears,
therefore, that (1) ypsiloid cartilage is of later origin than the
differentiation of the muscles associated with it, and (2) that it
arises as an unpaired structure in association with these muscles
and at a time when the girdle itself still exhibits its paired nature.
*It cannot, therefore, be interpreted as having arisen from the epi-
pubic process, but must be regarded as an independent chondrifica-
tion in association with differentiations of the innermost portion of*

*the rectus abdominis muscle in
the two somites immediately an-
terior to the pelvic girdle.*

Larvæ of both *Spelerpes*
and *Desmognathus* show, as do
those of lunged forms, an
early differentiation of the *M.
ypsiloideus posterior.* As in
the adult lungless forms the
fibers of this muscle insert, in
the absence of the ypsiloid car-
tilage, into the linea alba of
the first somite.
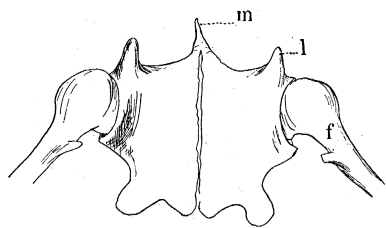
FIG. 9.   Ventral view of the pubo-
ischium of *Desmognathus fusca* larva (21
mm.) obtained by maceration, × 25.
Drawn with camera.   Abbreviations: *f*,
femur; *l*, lateral process; *m*, median proc-
ess, at this stage the only median part.

I had thought it possible that these larval stages might even
show a vestige of the ypsiloid cartilage itself, and there is, in
fact, some indication that such may be the case though I have as
yet been unable to obtain the stage necessary to absolutely prove
it.   The union of the two halves of the pubis begins at the ex-
treme anterior end, thus forming the future median anterior proc-
ess of the pubis.   This union (Fig. 9) appears to occur, not as
a direct fusion of the two halves by the process of chondrifica-
tion of the connective tissue between them, but rather by a fusion
of each half with a median unpaired anlage, which lies in the
linea alba anterior to the girdle.   Thus in transverse section this
median portion shows no trace whatever of a paired nature, a
fact which is especially significant when the condition is compared
with that of *Necturus* larvæ in which the median anterior process of
the pubis (*Processus epipubicus*) shows a paired nature even to its

extreme end.   However, I have not succeeded in obtaining either a *Spelerpes* or a *Desmognathus* of a stage just previous to the formation of this connection between the two halves of the pubis, and I am not sure, therefore, that the median unpaired portion ever exists as a separate cartilage arising like the ypsiloid cartilage anterior to the pelvic girdle and independent of it.   If it has such a separate origin it is undoubtedly a vestige of the stem of the ypsiloid cartilage.

C. *The Homology of the Ypsiloid Apparatus.*

There are two diametrically opposed views as to the homology of the ypsiloid cartilage.   One of these is that indicated by the quotations given earlier in this paper, viz., that the *Cartilago ypsiloides* is the homologue of the median anterior process of the pubis (*Processus epipubicus*) such as is found either single or paired in certain of the *Perennibranches* and *Derotremes*.   Moreover, this homology is extended to include the similarly situated process in various *Selachians*, *Ganoids* and *Dipnoans*.   This opinion as to the homology of the ypsiloid cartilage has been held very strongly by C. K. Hoffmann ('73–'78) and R. Wiersheim ('92) and corroborated by certain observations of H. Riese ('91).   Aside from general similarity of location of the ypsiloid cartilage and the *Processus epipubicus* the homology is apparently based upon a continuity of the cartilage tissue of the pubis with that of the stem of the ypsiloid cartilage.   This condition is, as has been shown, not the usual one in the adult, although Riese ('91) found it to exist in *Tylototriton verrucosus*, and Wiersheim has noted in the case of old individuals of other species a condition which he designates as a secondary fusion.   Wiersheim says, however, regarding the adult condition, that " Man bei histologischer Untersuchung in Allgemeinen viel häufiger auf verbindende Knorpelbrücken zwischen der Hauptmasse des Beckens und dem Epipubis stösst, als man dies nach der einfachen Präparation mit Messe und Pincette erwarten sollte."

In *Triton alpestris* larvæ Wiedersheim found, as I have done, that the ypsiloid cartilage arises by an independent anlage, but in larvæ of *Triton helveticus* and in a 26 mm. Axolotl he found the cartilage element continuous, although he adds : " Diese

Verbindungszone bestand im vorliegenden Fall nur ventralwärts und werde weiter dorsalwärts d. h. gegen das Cavum pelvis zu durch zellreiches Bindgewebe ersetzt." He finds, moreover, that " Um diese Zeit stellt das Epipubis eine auf dem Vorderand der Beckensymphyse aufsitzende spitzhöckerige, durchaus unpaare Vorwölbung dar, welche nur langsam zapfenartig nach vorn auswächst, und sich erst verhältnismässig spät in die schon erwähnten zwei Äste gabelt." The movable articulation of the *Cartilago ypsiloides* is then, according to Wiedersheim's interpretation, a secondary condition.

That there is, on the other hand, an apparent inconsistency between this idea of the homology of the *Cartilago ypsiloides* and the well-established fact of the paired nature of the anlage of the pelvic girdle, Wiedersheim at least tacitly admits when he says : " Die Verwischung des ursprünglichen Verhaltens prägt sich nämlich bei Salamandrinen in dreifacher Weise aus, erstens darin, dass hier von einer paarigen Anlage des Epipubis ontogenetisch nichts mehr nachweisbar ist, zweitens, dass zwischen diesem und dem übrigen Becken häufig eine Kontinuitätstrennung besteht, und drittens endlich, dass das kopwärts schauende Ende des Epipubis eine secundäre Formänderung, eine Gabelung, erfahren hat."

A further, and, in my opinion, insurmountable objection to this homology lies in Wiedersheim's own statement that the ypsiloid cartilage is of later origin ontogenetically than the girdle and makes its appearance as late as at the time when the midventral symphysis of the halves of the pubo-ischium is taking place.

The second view as to the homology of the *Cartilago ypsiloides* is that held by Bunge ('80) and Baur ('91) that the structure is developed wholly independently of the pelvic girdle to which it becomes secondarily articulated. With regard to this homology Bunge says :

" Es (the epipubis) ist eben eine Gebilde sekundärer Art, das ausschliesslich den Amphibien zukommt, wie ja Ähnliches auch bei anderen Wirbelthieren beobachtet werden kann, z. B. das Hypoischium der Saurier . . . Der Ansicht Wiedersheim's dass der Epipubis als ein erst sekundär von der knorpeligen *Pars*

pubica, resp. deren Verlängerung zur Symphysenbildung abge-
gliedertes Gebilde sein kann, da dasselbe sich als einheitlicher
Knorpel vor dem proximalen Ende der Symphyse anlegt, gleich-
falls nicht zugestimmt werden."

Baur, basing his reason upon the fact of the completely paired
origin of the true epigastroid (*i. e.,* epipubic) process, as shown
by *Necturus,* for example, draws the following very definite con-
clusion with regard to this unpaired, more anterior structure, the
Cartilago ypsiloides :

"I believe the ypsiloid cartilages are of secondary origin, de-
veloping independently from the gastroid (*i. e.,* pubic) cartilage.
The long epigastroid of the *Chelyiidæ* is homologue to the
short epigastroid in *Testudinidæ ;* homologue to the anterior
portion of the gastroid cartilage in *Necturus ;* homologue to that
portion of the gastroid in salamanders and *Dactyletra* to which
the ypsiloid cartilages are connected. I consider these cartilages
as a later acquisition and they may develop in any group, *Batra-
chia, Pterosauria, Monotremata, Marsupulia.*" So far, even, as
similarity in location between the *Cartilago ypsiloides* and the
epipubic process of the lower Urodeles is concerned, I have been
unable to find any ground for the homology. In none of the
Urodeles in which the *Cartilago ypsiloides* is lacking have I found
the epipubic process crossing even a single myotome of the
rectus abdominis. In *Necturus,* the form in which the epipubic
process is most conspicuously developed, there is merely a cor-
responding narrowing of the posterior myotomes of the rectus
abdominis, particularly the first one (Fig. 8).

Whether the ypsiloid cartilage is ever in any case continuous
with the pubis or not, it is very evidently a separate structure,
an independent chondrification of the linea alba of much later
origin than the pelvic girdle to which it sooner or later becomes
articulated. Thus considered, the ypsiloid cartilage presents no
obstacle to the idea of the paired nature of the anlage of the
pelvic girdle. Its existence is moreover explained quite in ac-
cordance with the principle which accounts for the origin of
similar structures (*e. g.,* the sternebræ of *Necturus*) in those con-
nective tissue regions where especially strong origin or insertion
of the muscle fibers is necessary. I have not had the opportunity

to study either the anatomy or the habits of *Dactyletra* in which
an apparently similar cartilage to the *Cartilago ypsiloides* is formed.
and can therefore express no opinion as to this homology.

That the *Cartilago ypsiloides* of salamanders is homologous
with the marsupial bones of *Monotremata* and *Marsupulia* is a
view which has been considered so completely established that
Dugés ('55) named this cartilage in salamanders the "marsupial
cartilage." Huxley also accepted this idea of its homology and
it is one of the principal points made by Wiedersheim ('92) in his
Phylogenie der Beutelknochen, in which, of course, this interpre-
tation is quite consistent with his idea that both the ypsiloid
cartilage and the marsupial bones are differentiations of the epi-
pubic process. Moreover, the acceptance of this homology is
indicated in the various names which have been given to the *M.
ypsiloideus posterior*, such as pyramidalis (Hoffmann). Leaving out
of account the question as to whether the ypsiloid cartilage and
marsupial bones are of similar origin so far as the pelvic girdle
is concerned, the supposed homology between the two is dis-
proved by their relations to the rectus abdominis muscle. The
ypsiloid cartilage lies dorsal to the main mass of this muscle ;
the marsupial bones are, of course, ventral to it. A comparison
of musculature, therefore, shows the lack of homology of the
ypsiloid apparatus with the marsupial. The musculature of the
ypsiloid cartilage is derived from the deeper layers of the rectus
abdominis and from the transversalis ; from the very poistion of
the marsupial bones, on the other hand, it is evident that the
musculature of this apparatus is derived from the superficial ab-
dominal muscles.

The pyramidalis, which has been homologized with the *M.
ypsiloideus posterior* is, for example, the most superficial portion
of the rectus abdominis. Further, it is on the wrong side of the
marsupial bone to make the homology a consistent one through-
out, since, if the marsupial bones correspond to the lateral arms
of the *Cartilago ypsiloides*, a muscle to be the homologue of the
M. ypsiloideus posterior must extend from the outer edge of the
marsupial bone to the pelvis, not as does the pyramidalis, from its
medial side to the linea alba or sternum. The pyramidalis and
the posterior ypsiloid muscle are then homologous only in the

very general sense that both are differentiations from the rectus abdominis ; they are differentiated from different layers and in connection with structures which are not themselves homologous. They are, in other words, independent differentiations occurring in widely separated forms and in response to absolutely different physiological needs.

PART II. THE FUNCTION OF THE YPSILOID APPARATUS.

A. *Respiratory Habits of Lunged Salamanders.*

Beyond the statement of the very evident fact that the ypsiloid cartilage furnishes the attachment for certain of the abdominal muscles (Wiedersheim, '75), I have been unable to find, in the literature upon the subject, any explanation of its function.   There is, however, as has already been said, so apparent a correlation in the *Salamandrida* between the presence of the apparatus and that of the lungs, that the explanation of its function will involve, first of all, a discussion of the respiratory habits of lunged salamanders.

The more obvious respiratory movements of lunged salaman-ders when breathing air have been very clearly described by Bruner ('96).   In brief, two forms of aerial respiration occur, one merely a bucco-pharyngeal, the other a pulmonary respiration. Both of these may be readily observed in the case of any lunged salamander.   The first takes place almost constantly and with great rapidity.   It begins with an enlargement of the bucco-pharyngeal cavity by lowering the hyobranchial apparatus ; this results in air being drawn in through the nares.   Following this inhalation is an exhalation in which the floor of the mouth rises again.   These movements follow each other so quickly that the visible effect is a rapid fluctuation of the throat.   The mouth remains tightly closed during the entire process, and the respira-tory currents make use of the nasal passages alone.

At frequent, though irregular intervals, during bucco-pharyn-geal respiration, acts of pulmonary respiration occur.   These are easily distinguished externally from the bucco-pharyngeal form by the fact that the depression of the floor of the mouth is a prolonged and exaggerated one, during the latter part of which a contraction of the *M. constrictor naris* occurs.   According to

Bruner, the effect of this contraction is to completely close the external naris. My own observations of *Diemyctylus* and the *Amblystomas* made by the aid of a lens do not, however, corroborate this statement, since I have frequently seen the external nares fail to close completely during pulmonary respiration, although there is always an almost complete closure.

As a result of the prolonged depression of the floor of the mouth air is first drawn in through the open nares, as in bucco-pharyngeal respiration. This part of the process is known as aspiration. During the latter part of the act of depression, however, when the external nares are closed, air is drawn from the lungs into the mouth through the opened glottis and the air in the mouth thus becomes a mixture of pure and impure air. This part of the process is termed expiration. When the floor of the mouth rises again some of this mixed air is forced into the lungs, the external nares being still closed. This constitutes the process of inspiration. Finally the external nares are opened again, and the fluctuating movements of bucco-pharyngeal respiration are resumed.

In addition to these two methods of aerial respiration the lunged salamanders which have come under my observation possess, when in the water, an *aquatic* bucco-pharyngeal respiration.

The Gages ('86*b*, '91) have reported such an aquatic respiration for *Diemyctylus* as well as for some of the lower *Urodeles*. Their statements are, however, indefinite as to the exact method by which the water is alternately taken into and expelled from the mouth. O. P. Hay ('89) seems to have made more exact observations upon *Amblystomas*, of which he says that " streams of water are drawn in through the nostrils and this water is then expelled at intervals by the mouth." This is precisely the method of bucco-pharyngeal respiration of water which I have many times verified with a lens by the aid of solid particles (carmine or sediment) suspended in the water in which specimens of *Diemyctylus* and *Amblystoma* were submerged. The muscular act seems to be exactly the same as in the bucco-pharyngeal aerial respiration, but owing to the heavier fluid the act is a much slower one, though varying in depth and rapidity with the activity of the specimen, as the accompanying tabulation of observations

shows. Moreover, the expulsion of water takes place through the slightly opened mouth as well as through the nares. *Amblystoma opacum*, which is said to be the most terrestrial of all the *Amblystomas*, showed the least readiness to adopt this aquatic mode of respiration, the pharyngeal movements being very feeble as if they occurred in response to an almost forgotten instinct. They are probably not of sufficient respiratory value to support life, since these specimens die in a short time if compelled to remain in the water.

RECORD OF OBSERVATIONS OF AQUATIC BUCCO-PHARYNGEAL
RESPIRATION IN DIEMYCTYLUS VIRIDESCENS.

(In each experiment a different individual was used.)

No. of Experiment.	Average No. of Respiratory Acts per Minute.	Largest No. for One Minute.	Smallest No. for One Minute.	Duration of Experiment in Minutes.	Nature of Respiratory Acts.	Activity of Specimen During Experiment.
No. 1.	21.4	23	19	10	Shallow.	Slightly active.
No. 2.	15.14	20	11	7	Deep.	Inactive.
No. 3.	10.04	13	9	5	[Not recorded.]	Slightly active.
No. 4.	8	18	3	10		

Detailed Record for Each Minute of Experiment No. 4.

	4				Very shallow.	Inactive.
	9				One very deep.	Walking slowly.
	3				Very deep.	Inactive.
	12				Shallow.	Active.
	4				Deep.	Inactive.
	9				Shallow.	Inactive, after a period of activity.
	18				Shallow.	Active.
	6				One very deep, ending in a prolonged gape.	Inactive.
	3				Very deep.	Inactive.
	12				Shallow.	Slightly active, following a period of great activity.

RECORD OF OBSERVATIONS OF AËRIAL BUCCO-PHARYNGEAL AND
PULMONARY RESPIRATION IN DIEMYCTYLUS VIRIDESCENS.

No. of Experiment.	Average No. of Bucco-phar. Resp. per Min.	Largest No. for One Minute.	Smallest No. for One Minute.	Average No. of Pulmonary Resp. per Min.	Largest No. for One Min.	Smallest No. for One Minute.	Duration of Observations in Minutes
No. 1.	187.7	213	145	1.1	4	0	10
No 2.	125.75	146	104	[Not recorded.]			4

The method of change of respiratory habit necessitated by the transition from one median to the other is interesting. When a *Diemyctylus* which has been breathing air is submerged in water, bucco-pharyngeal respiration of water begins almost at once. *Amblystomas*, being less thoroughly aquatic, postpone this change of habit for a longer or shorter time. The nares in this case are at first tightly closed and if the animal is kept submerged for only a few minutes it may not establish aquatic respiration at all. When a specimen which has fully established the aquatic habit of respiration is taken from the water there is evinced more or less mechanical difficulty in reëstablishing the aërial habit. This difficulty arises from the fact that the nasal passages are filled with water which must be removed before rapid, unimpeded respiration of air can occur. The efforts to do this involve forced and greatly exaggerated depressions of the floor of the mouth, a device which may prove efficacious in two ways, first, by drawing the water from the nasal passages into the mouth, and second, by drawing from the lungs a supply of air which can be used to force the water out of the nasal passages through the external nares. The transition from aquatic to aërial respiration may thus involve much effort and a considerable loss of time. I have observed specimens of *Diemyctylus* to consume ten minutes or more before perfectly normal aërial respiration was established. *Amblystomas* make the transition more quickly.

In connection with this mechanical difficulty of rapid transition from aquatic to aërial respiration, some lunged salamanders, notably *Diemyctylus*, have acquired for use when in the water a modification of the ordinary method of pulmonary respiration. Frequently air must be taken into the lungs during the brief period when by a rapid swimming to the surface, sufficient momentum has been acquired to force the head for an instant out of the water. It is evident that under these conditions the nostrils are utterly useless as air passages, as they are filled with water. Moreover, even if they were empty of water, or could be emptied in so brief a time, the ordinary method of drawing in air through such narrow passages is far too slow to be made use of here. The method employed is, therefore, a quick, gulping motion by means of which the water in the mouth is replaced by

air. This is immediately followed, as the head again returns into the water, by a forcible swallowing motion as a result of which the air is forced from the mouth partly into the lungs and partly out through the nostrils. Of those species the habits of which I have studied, *Diemyctylus viridescens* accomplishes with the greatest ease the act of taking air into the lungs in this way, an observation quite in harmony with the fact that *Diemyctylus* has the reputation of being the most thoroughly aquatic of our American salamanders.

The Gages ('86*a*, *c*) have shown that, in general, an animal having a mixed aquatic and aërial respiration depends mainly upon the latter for its supply of oxygen. I am not convinced, however, that this is of necessity true in the case of lunged sala-manders living under aquatic conditions. *Diemyctylus* and the *Amblystomas*, it is true, not only swim frequently to the surface and take in air, but, if it is possible, will partly crawl out of the water and for a shorter or longer time each day will breathe air normally. However, to test the absolute physiological necessity for aerial respiration, I experimented as follows : Several speci-mens of *Diemyctylus* were enclosed in small wire cages which were immersed to a depth of about 15 inches in a small tank of running water. To prevent the collection of bubbles of air upon the inside of the wire, the cages were frequently shaken to remove the bubbles while they were still too small to be used in breath-ing and thus vitiate the experiment. To ensure this frequent agitation during the night when personal attention to the matter was inconvenient, I used the simple device of placing a large and lively specimen of *Necturus* in the tank with the cages. The *Necturus*, being nocturnal in its activities, accomplished quite as efficiently the duty of keeping the cages free from air as was done during the day time by my own exertions. The precaution was taken, moreover, to make it impossible for any activity of the *Necturus* to lift the cages out of the water.

For periods varying from seven to ten days specimens of *Die-myctylus* were thus kept completely submerged and they remained in an active condition and apparently suffered no inconvenience as a result of the experiment. The capillaries of the skin, however, as observed by means of a lens, were much more distended with

blood than those of a specimen which had meanwhile lived a free aquatic life with access to the air. Apparently the skin, which, being supplied with capillaries may be looked upon as an accessory respiratory apparatus, had proved itself, in the emergency, equal to the extra demand made upon it.

An interesting effect of the disuse of lungs in this experiment showed itself in the great difficulty with which specimens, thus confined to the water, reëstablished the habit of filling the lungs with air when they were released from their imprisonment. Ordinarily, when a *Diemyctylus* swims to the surface and takes in air by the gulping process already described, there is an abundant visible proof of the fact that air has entered the lungs in the increase in girth of the body and especially in the immediate increase in buoyancy to such an extent that the specimen which before had been able to sustain itself in the water only by active swimming, suddenly becomes lighter than water and passively floats. When, however, specimens which had for several days been prevented from using their lungs were once more set free in the water and swam to the surface, although great gulps of air were taken, there was not the usual subsequent increase in buoyancy and the air escaped immediately in large quantities from both nostrils as the head sank again below the surface of the water. The effort to fill the lungs was repeated many times interspersed with intervals of rest lasting 15 or 20 minutes, so that several hours elapsed before any effect seemed to be produced upon the disused lungs. One could from the fruitless efforts of the animals imagine the lungs in a collapsed condition, the inner surfaces in contact with each other, and therefore resisting the entrance of air; and such, indeed, was found to be the case in other specimens which had been similarly confined under water and then killed without having had access to the air.

B. *The Hydrostatic Habits of Lunged Salamanders.*

Having discussed the various methods of respiration of lunged salamanders we are now prepared to describe those particular habits which involve, as will be shown, the use of the ypsiloid apparatus. Since my more extended observations have been made upon *Diemyctylus viridescens*, this species is the one which

will be referred to almost exclusively in the following discussion.

As has been said, the adult *Diemyctylus* is the most aquatic of our American salamanders. To anyone who has observed, even casually, the activities of this little animal in the water, its absolute ease under aquatic conditions must have been evident. If the specimens are in a deep aquarium this physical ease is very readily observed. Occasionally they may be seen at the bottom where they walk about or take rapid little swims to higher levels from which, as soon as the swimming motions cease, they passively sink to the bottom again. More often they may be found at the very surface of the water where they float with great ease or rest upon the aquatic plants, sometimes supporting themselves upon these by the fore limbs and lifting the entire head above the water. Frequently, moreover, they will be seen suspended in the water at a greater or less depth, where they have the power to swim lazily to and fro with hardly a perceptible muscular action, to paddle about, using all four feet as propellers, or to dart swiftly through the water by means of a rapid lashing with body and tail, the legs meanwhile being closely pressed to the sides of the body. For many minutes they will sometimes remain absolutely motionless in the water, the body kept in place by the mere contact of a foot, or even of a single toe, with some plant or other stationary object.

These facts indicate that while the specific gravity of *Diemyctylus* is never far from one, it varies slightly, as shown by the passive sinking, suspension or floating of the body at different times. What are, then, the mechanical means by which these changes in buoyancy are accomplished?

If our observations begin with a *Diemyctylus* at the bottom of the aquarium, with a specific gravity greater than one, it will be found that sooner or later the animal will swim rapidly to the surface, and, by the modified process of pulmonary respiration already described, will take into the lung sufficient air to cause the body to float (Fig. 10, *b*), the minute portion of the back which appears above the surface bearing witness to the fact that the specific gravity has now become slightly less than one. The animal may remain in this condition for a longer or shorter time. If he swims to a lower level, the moment his motions cease his body

rises slowly to the surface again.   Usually, however, the increase of buoyancy is soon followed (within a minute or two) by the emission from the lungs through the mouth of one tiny bubble of air after another, seldom more than two or three in all, until his buoyancy is so perfectly adjusted that his specific gravity is exactly one.   In this condition he can go about at ease, or remain motionless at any depth, and it is apparently only when he desires to sink to the bottom and remain there with some stability that by the emission of still more air the specific gravity is made sufficiently great to serve the purpose.   There always occurs, however, a gradual loss of buoyancy even when there is no further emission of air, a loss which I have never observed to be made good until the animal again swims to the surface and takes in more air.[1]

Diemyctylus shows a still further delicacy of adjustment to its aquatic environment, since, under any condition, whether floating, suspended in the water or resting on the bottom, there is the power to change, without the slightest swimming motion, the direction of the long axis of the body.   This adjustment may be best observed when the animal is suspended motionless in the water ; since then all other factors which produce change of position are eliminated.   The usual position of *Diemyctylus* when thus suspended is one in which the anterior end of the body slants slightly downward (Fig. 10, *b*).   From this position the whole body, without the slightest bending, may swing through a vertical angle of perhaps 30° until the head is directed upward instead of downward.   This change of direction is accompanied by a striking change in the shape of the animal.   When the poise is such that the head slants downward, there is a pronounced bulging of the lateral and ventral walls of the posterior third of the body cavity, particularly noticeable in the angle between the ilium and the vertebral column, as though some mechanism within were exerting an outward pressure.   As the

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[1] This phenomenon of loss of buoyancy without the emission of air is worthy of careful investigation.   It is probably not attributable to a mere compression of air (as in the case of the air-bladder of the fish), since there is no subsequent increase of buoyancy without taking in more air.   It must be due to an actual loss of gas from the lungs, probably owing to the excess of the volume of oxygen used over that of CO_2 and other gases given back to the lungs.

body swings upward, however, there occurs a marked constric-
tion of the posterior part of the abdominal cavity, often so pro-
nounced that the ventral wall (that is, the ypsiloid region) is
drawn sharply upward (Fig. 10, *a*).   In this condition the ventral
contour of the body exhibits an angle between this posterior and
the more anterior region.   These changes of shape may best be
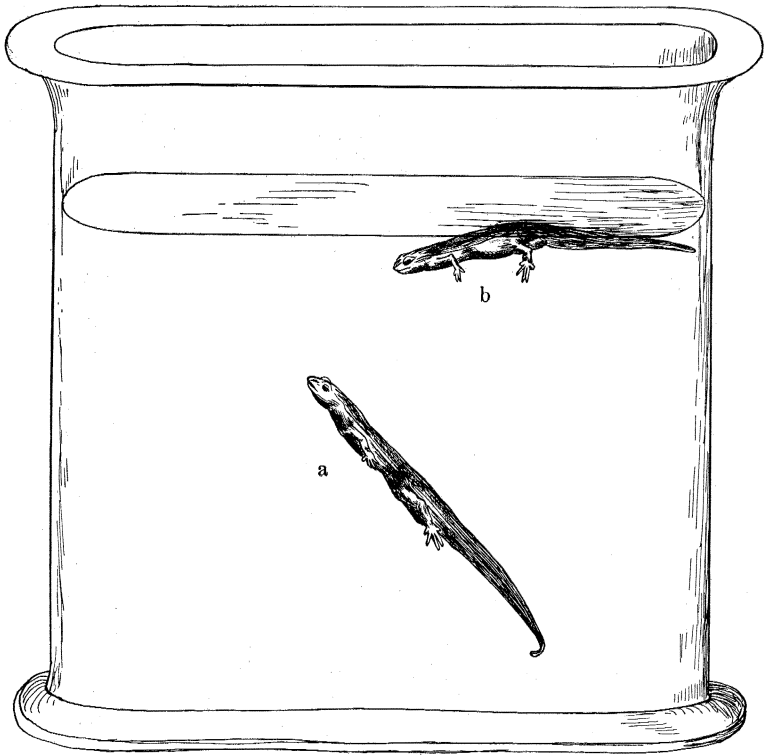
FIG. 10.   *Diemyctylus viridescens;* (*a*) showing the body directed upward in
swimming as a result of the compression of the posterior portion of the body cavity
through the action of the ypsiloid apparatus; (*b*) showing a characteristic floating
position with the posterior portion of the body cavity expanded and the anterior end
of the body depressed.

seen in a specimen which has not been fed for several days, since
they are partially masked by the presence of masses of food in
the digestive tract.

They occur, moreover, not only during this inactive change in
the direction of the long axis of the body, but changes of direc-

tion during active swimming involve a constant exhibition of corresponding changes of contour ; the constriction of the posterior abdominal region occurs when the swimming motion is upward (Fig. 10, *a*), the prominent bulging when the motion is downward. Further, a sudden change from a downward to an upward direction is *preceded* by an exaggerated constriction of the posterior part of the cavity, an act which conspicuously involves the sudden vigorous inpulling of the ypsiloid region. Evidently *there is in operation some mechanism for controlling the direction of the body, whether at rest or in motion, through the control of the relative buoyancy of anterior and posterior ends.*

C. *The Hydrostatic Mechanism of Lunged Salamanders.*

Turning now to the anatomy of the ypsiloid region, the explanation of this hydrostatic mechanism becomes very simple. The contraction of the *M. ypsiloideus posterior* exerts a strong pull upon the whole ypsiloid cartilage. The origin and insertion of this muscle are, however, so nearly in the same plane as the fulcrum (the articulation of the ypsiloid cartilage with the pubis) that it seems at first a question as to whether the cartilage would be bent upward or downward (*i. e.*, dorsally or ventrally) by the contraction of this muscle alone. It must be remembered, however, that the muscle is inserted into the upper (dorsal) surface of the stem of the cartilage and also that the more strongly developed portion of the muscle has its origin in the lateral portion of the pubis, a region which owing to the convexity of the body is slightly higher (more dorsal) than the insertion of the muscle and the articulation of the cartilage. Moreover, outside of the whole apparatus there are muscular walls (external oblique and rectus abdominis) which would resist any tendency to bend the cartilage downward, and with origin and insertion on so nearly the same plane as the fulcrum it requires only a slight resistance of this sort to turn the scale. Other muscles, moreover, are attached to the ypsiloid cartilage and coöperate with the ypsiloideus posterior to determine the direction of motion. The contraction of the ypsiloid portion of the transversalis exerts a decided upward (dorsalward) pull upon the ypsiloid cartilage while the anterior ypsiloid muscle, pulling upon the arms of the cartilage

from the linea alba, at least lends a certain steadiness to the apparatus while at the same time it coöperates with the ypsiloideus posterior and the ypsiloid portion of the transversalis to pull the arms strongly inward.

Corroboration of the above explanation is furnished by those occasional specimens which happen to have been preserved with the ypsiloid muscles contracted. These cases show that the effect of the concerted contraction of the muscles associated with the ypsiloid cartilage is not only to bend the stem of the cartilage upward (dorsally) at its articulation with the pelvic girdle but to curve the flexible arms upward and inward (medially). Evidently the result of the contraction of the three pairs of muscles connected with the ypsiloid cartilage is a decided constriction of the posterior region of the abdomen and a consequent compression of the organs contained within it.

To understand in what way this action of the ypsiloid apparatus controls the relative buoyancy of the anterior and posterior regions of the body, the shape and position of the lungs must be considered. The lungs of *Diemyctylus* are exceedingly simple structures, mere sacs with no trace of the usual amphibian condition in which the cavity is subdivided by partial partitions. It seems impossible, in fact, that such very simple structures with so small a supply of blood can justify their existence merely as respiratory organs. In shape, also, the lungs of *Diemyctylus* are peculiar. Narrow anteriorly, they widen gradually and round off quite abruptly at the posterior end. The whole form is most adequately described, perhaps, as club-shaped. The statement often given as to the size of the lungs (viz., one third to one half of the length of the body cavity) I find quite incorrect when the observations are made upon freshly killed specimens. If the lungs of such a specimen be inflated through the glottis not even sufficiently to float the body in water (and therefore not unduly), subsequent dissection shows that the lungs extend the entire length of the body cavity so that their rounded, bulging, free ends lie on either side in the angle between the ilium and the vertebral column.

It is thus easy to see the cause of the bulging of the lateral and ventral walls of the posterior part of the body cavity.

Moreover, it is also evident that with the lungs inflated and with no muscular constriction of this posterior region this portion of the body will possess greater relative buoyancy than the anterior portion, or in other words the long axis of the body will assume its ordinary position with the anterior end slanting downward. As soon, however, as the ypsiloid apparatus is brought into action, the resulting pressure upon the posterior abdominal organs becomes exerted upon the clavate ends of the lungs thus forcing the air in them forward. The effect is to immediately increase the buoyancy of the anterior region of the body and diminish that of the posterior region.

On the other hand, when the muscles relax, the pressure of the air in the lungs, as well as the elasticity of all the parts concerned, causes the return of the air to the posterior region again and the bulging of the body wall in this region occurs as before. It seems probable that the superficial portion of the rectus abdominis which is attached to the ventral side of the ypsiloid cartilage (its fibers extending from the lateral arms to the stem and to the anterior margin of the pubis), may assist in straightening the curved ypsiloid cartilage, since when the cartilage is in the bent condition these fibers lie upon its convex (ventral) side.

Thus the ypsiloid cartilage and the muscles connected with it constitute, together with the lungs, the mechanism by means of which the relative buoyancy of anterior and posterior ends of the body may be controlled. One needs only to witness the constant use of this hydrostatic apparatus by *Diemyctylus* to understand how completely the absolute ease of the animal under aquatic conditions is due to its power to control the direction of its body by means of the rapid adjustment of the relative buoyancy of anterior and posterior ends. The ypsiloid apparatus is thus of vital importance in the free-swimming aquatic life of a species which, like *Diemyctylus*, depends for its food supply upon its ease of movement in water at any depth.

Opportunity has not been afforded me to study extensively the aquatic activities of lunged forms other than *Diemyctylus*. Several specimens of *Amblystoma punctatum* and *Amblystoma opacum* [1] have, however, been observed with regard to this point. Both

[1] See p. 257 for statement with regard to the lungs of *Amblystoma opacum*.

of these species, although capable of much less perfect adjustment to aquatic life, resemble *Diemyctylus* in the fact that the lungs are used as hydrostatic organs.   Almost the first act of an *Amblystoma* when it is placed in deep water is to swim to the top and take in the air sufficient to float the body.   I have not observed an *Amblystoma opacum* to become sufficiently at home in the water to do more than to remain floating at the surface. *Amblystoma punctatum* will, however, after a little while, appear quite at ease, crawling about the bottom, floating at the surface, or swimming around with much freedom.

Although the greater thickness and breadth of the rectus abdominis of *Amblystomas* prevent the visible exhibition of the action of the ypsiloid region during aquatic life, changes of shape of the posterior lateral walls of the body are often observable. Upon one occasion a specimen of *A. punctatum* was observed floating in a horizontal position at the surface of the water.   Suddenly there was a violent contraction of the posterior abdominal walls particularly noticeable in the lateral region, and immediately the position of the body became so nearly vertical that the head was sufficiently protruded from the water to make aerial respiration through the nostrils possible.   This observation not only proved that the ypsiloid apparatus is functional in the control of the hydrostatics of *Amblystoma punctatum*, but it suggests the application of its action as a means for bringing the floating body into such a position that the respiration of air may occur.   In the case of imperfectly aquatic forms this use of the mechanism might at times be extremely important.   For example, *Amblystoma opacum* will frequently, if compelled to remain in the water, take this same almost vertical position at the surface with the nostrils out of the water and is thus able to breathe air.

That the lungs of *Amblystomas* are of greater importance as respiratory organs than are those of *Diemyctylus* is evidenced by the fact that they are more complicated in structure and therefore present a much larger respiratory surface.   They are, however, like the lungs of *Diemyctylus*, of sufficient length when moderately inflated to extend the entire length of the body cavity and would therefore lend themselves readily to the hydrostatic function in connection with the ypsiloid apparatus.

With regard to the relative importance of the lungs of sala-
manders as respiratory and as hydrostatic organs, it is a signifi-
cant fact that in no case have I found that a *Diemyctylus* or an
Amblystoma which was out of the water and using its lungs
normally in air-breathing, had sufficient air in the lungs to float
the body when it was dropped into water. Almost the first act
under these circumstances is to swim to the top and take in a
quantity of air sufficient to float the body. This indicates plainly
the secondary adaptation of the lungs as organs of buoyancy and
it is easy to see how in the case of a species like *Diemyctylus*
which has become thoroughly aquatic, the hydrostatic function
might become of so much greater importance than the respira-
tory as to account for the apparent degeneration of the lungs as
respiratory organs which is indicated by their simplicity of struc-
ture. Moreover, it is easy to understand how a mechanism such
as the ypsiloid apparatus for controlling relative buoyancy of the
anterior and posterior ends of the body, while useful to any lunged
form for the longer or shorter periods during which it normally
stays in the water, would become especially perfected in its action
in the case of a thoroughly aquatic species.

D. *Negative Evidence Furnished by Lungless Salamanders.*

In corroboration of the above conclusions as to the function of
the ypsiloid apparatus of lunged salamanders, we have the
negative evidence furnished by the habits of lungless forms in
which, with the single exception of *Salamandrina perspicillata*,
the *Cartilago ypsiloides* is apparently lacking.

These forms have, of course, no hydrostatic powers. They
are thus, unlike the lunged salamanders, incapable of a comfort-
able, free-swimming existence at any depth, but owing to lack
of hydrostatic organs they must remain for the larger part of the
time at the bottom. As Camerano ('94, '96) has pointed out,
although certain lungless species may be more or less aquatic,
their activities, even when in the water, are terrestrial. Various
species of *Spelerpes*, *Plethedon* and *Desmognathus*, for example,
will at first, when placed in an aquarium, swim to the surface,
then around and around the edge of the aquarium, as if seeking
a means of escape, but the instant that active swimming ceases,

the body sinks clumsily and heavily to the bottom where they remain until disturbed, or until another effort is made to escape.

Consistently with the lack of hydrostatic apparatus, lungless forms show on the whole, little power to adapt themselves to aquatic life.   Most of them are terrestrial in habit, some of them as, for example, *Plethodon cinereus* and *P. glutinosus*, being found far from any water supply, while the arboreal *Autodax* furnishes an extreme illustration of total abandonment of aquatic life. Those species, which, like *Desmognathus*, live along the banks of small streams, apparently never seek deep water, nor do they remain long submerged in shallow water, but often are found lying with the body in the water and the head (or at least the nostrils) out.[1]

Lungless forms, moreover, exhibit less adaptation to aquatic life in their respiratory powers, since unlike the lunged forms there is practically no aquatic bucco-pharyngeal respiration. When the animal is submerged, the nostrils, which have been widely open during aërial bucco-pharyngeal respiration, close at once and, so far as I have been able to carry my observations, the nares remain closed as long as the animal is in the water. In a few cases I have observed occasional feeble movements of the floor of the mouth, which were undoubtedly attempts at bucco-pharyngeal respiration, but even then the external nares were closed and the water was both drawn in and expelled through the slightly opened mouth.

Spelerpes ruber proved to be the most aquatic of all the lungless forms with which I experimented.   One specimen lived for weeks at the bottom of the aquarium and was never observed to attempt to come to the surface except when disturbed.   On the other hand, specimens of *Desmognathus fusca* invariably escape from the water when not caged, while *Plethodon glutinosus*, *Spelerpes guttolineatus* and *Spelerpes bilineatus* make frantic attempts to do so, but since they do not possess the power to crawl up the surface of the dry glass as *Desmognathus* does, their efforts are unsuccessful.   This aversion to aquatic life, is, however, apparently not due to an actual physiological need, for specimens of *Desmognathus fusca, Plethodon glutinosus* and *Spelerpes*

[1] See my article now in press on the "Naso-labial Groove of Lungless Salamanders."

guttolineatus suffer no physiological inconvenience when com-
pelled to remain under water as in the experiment described
above in which they were confined in wire cages immersed in
running water for a week or more without access to air. They
invariably, however, as soon as released, swam to the surface of
the water and tried to escape, thus showing a strong instinct to
seek terrestrial conditions even though their physiological needs
were satisfied. It cannot, therefore, be argued that the aversion
to aquatic life is due to lack of lungs and correlated ypsiloid
apparatus but rather that the long continued terrestrial habit has
resulted in the loss of these structures. An aquatic lungless
form like *Spelerpes ruber* must then be regarded as having sec-
ondarily reacquired its aquatic habits.

Salamandrina, a lungless form which possesses an ypsiloid
apparatus, is an interesting exception but by no means an em-
barrassing one, since it belongs to a wholly different group of
salamanders and thus represents a case of analogical resemblance.
It might be expected *a priori* to show less divergence in structure
from the lunged salamanders than do the members of the families
Plethodontidæ and *Desmognathidæ*, since its departure from the
habits of the rest of its own family, the *Pleurodelidæ*, is presum-
ably comparatively recent. Thus we find that it still possesses
arytenoid cartilages and rudiments of lungs. Similarly the ypsi-
loid apparatus persists, though Wiedersheim ('75) called attention
to the fact that the cartilage is less strongly developed than in
the case of *Triton* in which it usually undergoes more or less
calcification. There are additional evidences in the condition of
the muscles of the region (already described) that slight degen-
eration of the apparatus has taken place.

Of course a secondary adaptation to some other function might
tend to preserve the apparatus, but as I have not yet had the op-
portunity to observe the living *Salamandrina* I can make no
statement as to the probabilities of such secondary adaptation.

E. *The Hydrostatic Functions of Perennibranches and Derotremes.*

The following table expresses briefly the conditions of lower
Urodeles with reference to the possession of lungs and ypsiloid

apparatus, together with a general description of body form and habits : [1]

Name.	Lungs.	Ypsiloid Apparatus.	Form of Body.	Habits.
Necturus.	Present.	Wholly lacking.	Short and broad with compressed tail.	Lives largely on bottom. Floats only under abnormal conditions, *i. e.*, when water becomes foul.
Proteus.	Present.	Cartilage lacking; facts concerning musculature unknown.	Slender with compressed tail.	Facts unknown.
Siren.	Present.	Wholly lacking.	Slender and eel-like.	Burrows and swims.
Typhlo-molge.[2]	Lacking.	Cartilage lacking; facts concerning musculature unknown.	Slender.	Crawls about at bottom.
Axolotl.	Present.	Present.	Short and broad; tail compressed.	Swims.
Crypto-branchus.	Present.	Present.	Short and broad; tail compressed.	Swims; is said to come frequently to the surface for air.
Amphi-uma.	Present.	Wholly lacking.	Slender and eel-like.	Burrows, swims with great ease and comes frequently to the surface for air.

A comparison of the facts given in this tabulated form shows that the following classifications may be made :

1. Forms with lungs and ypsiloid apparatus — *Axolotl, Cryptobranchus.*

2. Forms with lungs but without an ypsiloid apparatus — *Siren, Necturus, Proteus, Amphiuma.*

3. Forms with neither lungs nor ypsiloid apparatus — *Typhlomolge.* Of the first group it may be said that since *Axolotl* is a larval form of a salamander which has lungs and an ypsiloid apparatus, its condition is exactly what one would expect to find

[1] The statement of facts relating to the habits of these forms is the result of my own observation only in the case of *Necturus* and *Amphiuma*. In other cases the information has been derived from various scientific works.

[2] Miss Emerson (1905) has shown valid reasons for regarding *Typhlomolge* the permanent larval form of one of the *Plethodontidæ*.

from the facts already given as to the development of the ypsi-
loid apparatus in other *Amblystoma* larvæ. Moreover, the lungs
are doubtless functional as hydrostatic organs and the ypsiloid
apparatus probably serves its usual purpose in controlling this
function.

I have not had the opportunity to observe the habits of *Cryp-
tobranchus*. From the descriptions which have been given of its
habits, however, one can readily believe that its lungs and ypsi-
loid apparatus are important, functionally, as hydrostatic organs.
The large size of the ypsiloid cartilage and the well developed
state of its muscles is, in itself, an indication of its functional
value. Moreover, the body is relatively short and the three pos-
terior somites of the trunk, that is, the region which would be
constricted by the action of the ypsiloid apparatus, form a suffi-
ciently large proportion of the entire length of the body to
render such constriction effective.

With regard to the second group two general types of body
form may be observed — the short, stout, heavy body of *Nec-
turus*, and the eel-like form such as *Amphiuma* and *Siren*. Cam-
erano ('96), has expressed his belief that in all these forms the
lungs have an important hydrostatic function. My own obser-
vations of the living animals have been confined to *Necturus* and
Amphiuma. The former I have never observed to float except
upon one or two occasions when the water has become very
foul. Under ordinary conditions the *Necturus* in captivity stays
at the bottom of the aquarium, often hiding in crevices between
rocks. Occasionally, especially if much disturbed, it will swim
to the surface and take in air through the mouth by a gulping
motion. This is usually followed by an immediate escape of air
through mouth and gill-slits as the animal sinks slowly to the
bottom. Undoubtedly the natural habitat of *Necturus* is at the
bottom ; it has, therefore, no use for an apparatus controlling the
hydrostatic function of the lungs. Moreover the total lack of
all traces of an ypsiloid apparatus indicates at once that the
species has not descended from one with such an apparatus,
since the muscular vestiges in wholly lungless forms show how
very slowly the degeneration of such an apparatus occurs.
Neither can we believe that the *Necturus* is a permanent larval

form of a lunged salamander, since such a larval form would certainly show traces of an ypsiloid apparatus. In this connection it may be noted that H. H. Wilder in a footnote to Miss Emerson's recent work on *Typhlomoge* (1905) stated that Kingsbury's (1905) suggestion that *Necturus* may be a permanent larva of one of the *Plethodontidæ* is untenable, since all of the *Plethodontidæ* are lungless. It now seems that in view of its lack of ypsiloid apparatus, *Necturus* is ruled out of all possible claim as a salamander larva.

My observations of *Amphiuma* give evidence of greater hydrostatic powers than in the case of *Necturus*. While this animal, like *Necturus*, spends its time largely at the bottom of the aquarium, burrowing if the mud is sufficiently soft, it occasionally comes to the surface of the water to breath air. To accomplish this, the tip of the snout is thrust out of the water, the body being sustained at the surface by its own active serpentine movements. Air is taken into the lungs by the process of pulmonary respiration already described for lunged salamanders. As the air enters, the buoyancy of the body increases perceptibly, often until the body actually floats. I have seldom, however, observed a specimen to retain this buoyant condition for more than a few minutes. It will swim down, allowing bubbles of air to escape as it goes, until it rests with its usual stability upon the bottom. I have sometimes observed, however, during these few minutes, marked constrictions of anterior or posterior body regions with corresponding changes of buoyancy of these regions, such changes apparently aiding somewhat in directing the eel-like motion of the animal. From my own somewhat limited observations I should conclude, however, that the lungs of the *Amphiuma* subserve mainly the respiratory function although there is a possibility of use for hydrostatic purposes. In any case it is very evident that an ypsiloid apparatus affecting as it does, only two or three body somites, would be practically useless as an accessory hydrostatic apparatus in the case of an animal with a long eel-like body comprising a very large number of somites like that of *Amphiuma*. This fact would in itself account for the lack of such an apparatus in these slender, eel-like forms, *Amphiuma* and *Siren*. The lack of all vestige of both ypsiloid cartilage and

muscles does not however as in the case of *Necturus* preclude the possibility of descent by degeneration from some higher lunged form, since the entire pelvic region shows numerous signs of degeneracy.

With regard to *Typhlomolge*, Miss Emerson (1905) has already shown conclusively the probability that this form is a permanent larva of a lungless salamander. Unfortunately I have not at hand the means for ascertaining whether in this form, as in the known *Plethodontidæ*, vestiges of ypsiloid muscles occur, but Miss Emerson mentions the failure of the cartilage as one of the characteristics of *Typhlomolge*. My proof that the use of the ypsiloid cartilage is correlated with the hydrostatic function of the lungs, therefore merely strengthens Miss Emerson's argument that *Typhlomolge* is the larva of a lungless form.

In conclusion, I wish to acknowledge my indebtedness to Dr. Harris H. Wilder for much practical assistance in the preparation of this paper.

SUMMARY.

1. The ypsiloid apparatus is, with the exception of *Cryptobranchus*, confined to the suborder *Salamandrida*. It has arisen in response to the physical need of controlling the direction of the body in water through the adjustment of the relative buoyancy of the anterior and posterior ends. Its function is therefore closely correlated with the hydrostatic function of the lungs.

2. In origin the ypsiloid cartilage is independent of the pelvic girdle. Its stem arises as a chondrification of the linea alba of the somite immediately anterior to the pelvic girdle. The arms are more complex in origin since the process of chondrification involves not only the myocomma anterior to the above named somite but also the outer edge of the aponeurosis of the transversalis muscle.

The *Cartilago ypsiloides* is therefore not homologous either with the *Processus epipubicus* of the lower *Urodeles* or with the marsupial bones of certain mammals.

3. In the *Plethodontidæ* and *Desmognathidæ*, in which the lungs have wholly degenerated, a correspondingly complete degeneration of the ypsiloid cartilage has occurred, although

vestiges of the ypsiloid musculature remain to indicate the former possession of the apparatus.

4. This interpretation of the function of the ypsiloid apparatus throws some light upon the systematic position of certain of the lower *Urodeles*. The more obvious conclusions are :

a. That forms with lungs but without vestiges of an ypsiloid apparatus, and with no evidence of degeneration in the pelvic region (*e. g.*, *Necturus*) are neither degenerate forms, nor permanent larvæ of any of the *Salamandrida*.

b. That the absence of the ypsiloid cartilage considered in connection with the absence of lungs in the case of *Typhlomolge* is in full accord with the conclusion [Emerson, 1905] that *Typhlomolge* is the permanent larva of some lungless salamander.

c. That the presence of a functional ypsiloid apparatus in *Cryptobranchus* indicates that *Cryptobranchus* lies near the line of descent of the *Salamandrida*.

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February 1, 1906.

POSTSCRIPT.

Since the above article was written, a paper on the Anatomy of *Cryptobranchus allegheniensis* by Reese has appeared in the *American Naturalist*, Vol. XL., No. 472. In this article the following statement is made :

"Anteriorly the pubis is prolonged into a long, cartilaginous *epipubis*, which, instead of being forked as in the Japanese salamander and some other Amphibia, is a straight rod, slightly broadened and flattened at its distal end and somewhat enlarged, both laterally and dorso-ventrally at its attached end. The union of the pubis and epipubis is a close one, but allows considerable freedom of motion."

The results of my own dissections (p. 264) are so completely at variance with this description of Reese's that I can but feel that he was mistaken in the form and character of the part in question. I have, however, based my description upon three specimens only, and it is possible that we have here to do with a case of marked individual differences ; but that all of my specimens should have the typical Y-form, while all of Reese's were rod-shaped, does not seem probable.   I. L. W.

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